Long-term spatial stability of coyote (*Canis latrans*) home ranges in southeastern Colorado

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Abstract: Long-term stability of territorial boundaries has not been well documented in canids. To evaluate the prevalence of long-term spatial stability of coyote (*Canis latrans*) home ranges, we compared the overlap of territorial boundaries and the spatial distribution of telemetry locations of packs in southeastern Colorado. From August 1983 to July 1988 (period 1), 16 coyotes from six packs were radio-tracked. From April 1996 to August 1997 (period 2), 12 coyotes from six packs were captured and tracked in the same area. Mean percentage of overlap of pack ranges was 89.8 ± 8.3% (±SD) for period 1 ranges over period 2 ranges and 55.8 ± 14.4% for period 2 ranges over period 1 ranges. Mean percentage of overlap of the 30% core area of the home ranges was 65.2 ± 13.9% for those of period 1 over those of period 2 and 66.3 ± 28.7% for those of period 2 over those of period 1. Despite substantial overlap of home-range and core-use areas, there were significant differences in the distribution of locations between periods in five of six home ranges. This suggests that, although packs are faithful to one site (i.e., boundaries remain similar over a period of years), their use of the site (i.e., distribution of locations within the range) may change temporally.

Résumé : La stabilité à long terme des limites territoriales chez les canidés est encore mal connue. Dans le but d'évaluer la stabilité spatiale à long terme des domaines chez le Coyote (*Canis latrans*), nous avons comparé le chevauchement des limites territoriales et la répartition spatiale des repérages télémétriques chez des meutes du sud-est du Colorado. D'août 1983 à juillet 1998 (période 1), 16 coyotes appartenant à six meutes on été repérés par radio. D'avril 1996 à août 1997 (période 2), 12 coyotes appartenant à six meutes ont été capturés et suivis dans la même zone. Le chevauchement moyen des meutes exprimé en pourcentage a été de 89,8 ± 8,3 % (écart type) dans le cas des domaines enregistrés durant la période 1 par rapport à ceux enregistrés durant la période 2 et de 55,8 ± 14,4 % dans le cas des domaines enregistrés durant la période 2 par rapport à ceux de la période 1. Le chevauchement moyen de la portion centrale (30 %) des domaines a été de 65,2 ± 13,9 % (période 1 sur période 2) et de 66,3 ± 28,7 % (période 2 sur période 1). En dépit du chevauchement important des domaines et des zones centrales, il y avait des différences significatives de la répartition des sites de repérage entre les périodes dans cinq des six domaines. Ces résultats indiquent que malgré la fidélité des meutes à un endroit (i.e., similitude des limites durant plusieurs années), l'utilisation de l'endroit (i.e., répartition des sites de repérage dans le domaine) peut changer temporairement.

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Introduction

Long-term spatial stability of home ranges in animals incorporates both individual site fidelity as well as the continued use of the site by members of the social group or population. Site fidelity among individuals has been documented in a wide variety of species, including birds (Greenwood and Harvey 1982; Lindberg and Sedinger 1998), mammals (Twiss et al. 1994; Law 1996), reptiles (Webb and Shine 1997), amphibians (Waldman et al. 1992), fish (Northcote 1997; Pellett et al. 1998), insects (Alcock 1996; Switzer 1997), and molluscs (Iwasaki 1995). The term site fidelity has been applied to various behaviors associated with repetitive or continuous use of previously occupied space, for example, repetitive return to breeding (Kavanagh and Murray 1996), nesting (Pledger and Bullen 1998), or feeding (Irons 1998; Weinrich 1998) grounds or faithfulness to a territory (Peterson et al. 1998).

The adaptiveness of home-range stability varies with a number of environmental and individual characteristics. Continued use of a site by an individual appears to be positively related to the cost of changing territories, age, previous reproductive success, and the probability of mortality in the habitat (Gratto et al. 1985; Switzer 1993). The benefits of site familiarity gained from continued use of an area include knowledge of foraging areas, shelter, and breeding opportunities. Frequent movement of territories may leave an animal vulnerable to unknown predatory pressures or aggressive conspecifics. Conserving energy for lactation and reducing juvenile mortality by maintaining familiarity with resource distribution may explain site fidelity in female red kangaroos (*Macropus rufus*) in arid western Australia (Norbury et al. 1994). Site fidelity in the ruff (*Philomachus pugnax*) is thought to facilitate stable dominance relationships, which are important to all territorial males using lek sites (Widemo 1997).

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In certain circumstances, however, site fidelity may not be adaptive. Site fidelity is likely to be inversely related to heterogeneity in territory quality and the animal's lifespan (Switzer 1993). Warkentin and Hernandez (1996) noted that species of nearctic–neotropical migrant songbirds that exhibit high levels of site fidelity might be less adaptable to habitat degradation and loss. This has important conservation implications, owing to the vulnerability of these species to population declines with the increases in deforestation of tropical zones. Strong site fidelity and small population size have been implicated in low within-island genetic variability, which has likely led to inbreeding in the endangered Hawaiian monk seal (*Monachus schauinslandi*) in the northwestern Hawaiian islands (Kretzmann et al. 1997). The high degree of site fidelity found in the threatened broad-headed snake (*Hoplocephalus bungaroides*) in Australia (Webb and Shine 1997) also has conservation implications. To facilitate recovery of the species, researchers were interested in the feasibility of natural recolonization of "restored" habitats. However, strong site fidelity, coupled with low rates of dispersal of juvenile snakes, mitigates against successful recolonization of rehabilitated habitats.

An understanding of the extent of long-term spatial stability of site use exhibited by an animal is important in making appropriate management and control decisions. For example, the commonly held belief among landholders in Australia is that dingoes (*Canis familiaris dingo*) travel 20–40 km to kill sheep (Harden 1985). However, studies have documented limited movements and strong site fidelity in dingoes, indicating that sheep depredations are likely to be caused by animals living on or adjacent to farms (Harden 1985; Thomson et al. 1992). Site-faithful behavior is important to pup-removal or reduction management techniques used for coyotes (*Canis latrans*), in which long-term site fidelity of sterile or otherwise nonreproducing coyotes (which are less likely to depredate sheep as they lack pups to feed) near properties reduces the likelihood of reproducing animals becoming established in the area (Till and Knowlton 1983).

The level and extent of site-use stability in canids has not been well documented. Peterson and Page (1988) and Peterson et al. (1998) reported that wolf (*Canis lupus*) packs on Isle Royale occupied territories for several years and that new packs occupied similar territories of previous packs. In these cases, the researchers hypothesized that a single non-collared wolf from the previous pack may have founded the new pack. Similarity was also evident in the spatial organization of the entire population, with space-use patterns in the mid-1980s resembling those of the early 1960s (Peterson and Page 1988), indicating that members of the wolves' social groups or population maintained ranges similar to those of previous territory holders. Fuller (1989) referred to the relatively stable, long-established territorial boundaries of wolves in north-central Minnesota. During a 10-year study, Thomson et al. (1992) found that dingoes in northwestern Australia exhibited strong site fidelity, rarely travelling far out of their territories. Studies of coyotes have indicated that some coyote packs remain in the same area for ≥1 year

(Bowen 1982; Bekoff and Wells 1986). We compared coyote home range distribution between 1983 and 1988 with that documented between 1996 and 1997 on the Pinon Canyon Maneuver Site, southeastern Colorado, to evaluate the prevalence of long-term spatial stability of coyote home ranges in a lightly exploited population.

Methods

The study area was located on the 1040 km² Pinon Canyon Maneuver Site (PCMS), Las Animas County, Colorado. The climate is semi-arid with a mean annual precipitation ranging between 26 and 38 cm. Mean monthly temperatures range from –1°C in January to 23°C in July. Elevations range from 1310 to 1740 m. The site consists of river canyons, limestone breaks, and open plains. The two main vegetation types are short-grass prairie and pinyon pine (*Pinus edulis*) – juniper (*Juniperus monosperma*) communities (Shaw et al. 1989). The study area was used primarily for cattle ranching prior to 1982, during which time predator populations (mostly coyotes and swift fox (*Vulpes velox*)) were subjected to trapping and hunting. In 1982, the U.S. Army acquired the PCMS for military activities that involved month-long mechanized training sessions 3–4 times a year. Coyote removal on PCMS was prohibited from 1983 to 1986. In 1987 and 1988, coyotes on the southwestern third of the site were controlled (Gese and Rongstad).[2] Trapping prior to 1982 and removal in 1987 and 1988 may have caused some instability in coyote packs. Since 1988, there has been no intensive removal, although occasional shooting of coyotes by hunters has occurred. Trapping and hunting of coyotes continues on the ranches surrounding the study area.

Coyotes were radio-collared and tracked from August 1983 to July 1988 (period 1) and from April 1996 to August 1997 (period 2) on the PCMS. In period 1, coyotes were captured using steel leg-hold traps, aerial darting (Baer et al. 1978), aerial net-gunning from a helicopter (Barrett et al. 1982; Gese et al. 1987), manual capture after aerial pursuit (Gese et al. 1987), or manual capture from all-terrain vehicles (Gese and Andersen 1993). In period 2, coyotes were captured by aerial net-gunning from a helicopter (Barrett et al. 1982; Gese et al. 1987). Each coyote was ear-tagged, aged by tooth wear (Gier 1968), sexed, weighed, and radio-collared. Transmitter mass was <5% of the body mass of the animal (Eberhardt et al. 1982). All radio collars included a mortality sensor that activated after 6 h of no motion. All coyotes were released at the site of capture.

Locations were obtained by triangulating 2–3 bearings of an animal's position within 10 min. Triangulation angles were maintained between 20° and 160° (Gese et al. 1988). Animal positions were determined using the software package Locate (Pacer Ltd., Truro, N.S.). Telemetry error was determined with reference transmitters to be ±8°. We attempted to obtain equal numbers of locations in all time periods throughout the day, to reduce bias in home range size estimates (Gese et al. 1990). Point locations were taken at ≥8-h intervals. Aerial telemetry (Mech 1983) was employed to locate missing animals. Coyotes were considered to be resident pack members if they were sharing the same territory (Gese et al. 1988).

Point locations were used to determine home-range size (Gese et al. 1990) and spatial distribution. A minimum of 100 locations per coyote pack was used in home-range estimation. Home-range size and spatial overlap were determined using Calhome home-range analysis program (Kie et al. 1996) and Arcview 3.0 (Environmental Systems Research Institute, Inc., Redlands, Calif.). Home-range

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sizes were calculated using the 95% adaptive kernel algorithm and core areas were calculated using the 30% adaptive kernel algorithm (Worton 1989). Core areas were assessed in addition to home ranges, to evaluate the spatial stability of high-use areas within the home range. The distance (kilometres) between the centroids of pack home ranges between the two periods and between seasons was also calculated.

Multiple response permutation procedures (MRPPs; Mielke et al. 1976) were used to examine changes in distributions of coyote locations or space-use patterns between the two periods, to elucidate changes in the internal structure of the home range. MRPPs compare the observed intragroup (for example, pack or season locations) average distances between any two locations with the average distances that would have resulted from all possible combinations of intergroup locations under the null hypothesis. Thus, the MRPP test statistic, δ, is a linear combination of average within-group distance measures for the n groups. The test does not assume normal distribution or equal variances (Zimmerman et al. 1985). MRPPs were also used to compare the distributions of coyote locations between seasons within a period (i.e., the seasons within period 1 were analyzed separately from those within period 2), to compare short-term as well as long-term changes in space-use patterns. For the purposes of analyses, we defined seasons on the basis of energetic demands (owing to climatic changes and prey abundance) and behavioral characteristics (including breeding, gestation, pup-rearing, and dispersal) as follows: pup-rearing season (15 April – 14 August), dispersal season (15 August – 14 December), and breeding–gestation season (15 December – 14 April).

As prey abundance can influence space-use and home-range patterns, estimates of prey abundance were obtained by spotlighting for lagomorphs. Spotlighting was done from a vehicle travelling 10–15 km/h along transects. Over 550 kms of transects were spotlighted in each period. Cottontail rabbits (*Sylvilagus audubonii*) and black-tailed jackrabbits (*Lepus californicus*) were identified, and both species were combined for analysis. The number of lagomorphs spotted per kilometre in surveys during the two periods were compared using Student's t tests.

Results

From August 1983 to July 1988, 16 coyotes (eight male, eight female) from six packs were located 988 times using radiotelemetry. The number of individuals from packs 1 through 6 in period 1 were three, three, three, two, two, and three, respectively. In 1996 and 1997, 12 coyotes (seven male, five female) were captured in the same area in which the coyotes of period 1 were captured. The number of individuals from packs 1 through 6 (pack number was designated by position of home range and corresponds between the two periods) in period 2 were three, two, two, two, one, and two, respectively. We collected 1923 locations of these coyotes from April 1996 to August 1997. Coyote-pack home ranges documented in period 1 overlapped those documented in period 2 (Fig. 1). The mean (±SD) percentage of overlap was 89.8 ± 8.3% for period 1 home ranges over period 2 home ranges and 55.8 ± 14.4% for period 2 home ranges over period 1 home ranges. The mean percentage of overlap for the 30% core area of the home-ranges was 65.2 ± 13.9% for those of period 1 over those of period 2 and 66.3 ± 28.7% for those of period 2 over those of period 1. The mean distance between the centroids of pack home ranges between periods was 0.86 ± 0.22 km (mean ± SE); this was not significantly greater than the distance between

centroids between seasonal home ranges within packs within periods (0.67 ± 0.11 km) ($t = 0.49$, df = 40, $P = 0.434$).

Even though period 1 and period 2 coyote home ranges were found to have substantial overlap, there was some variation between periods in the sizes of the home ranges for some packs. Overall, home ranges in period 2 were significantly smaller than those of period 1 ($t = 2.36$, df = 10, $P < 0.05$), with home ranges decreasing by as much as 59.84% (Fig. 1). On average, the home-range size decreased by 39.8%. Lagomorph counts in period 1 were found to be significantly smaller than those in period 2 (mean number of lagomorphs/kilometre ± SD = 0.36 ± 0.06 and 0.84 ± 0.26, respectively; $t = 4.24$, df = 75, $P < 0.001$).

MRPPs indicated a significant change in space-use patterns from period 1 to period 2 for five of the six packs (Table 1). MRPPs also demonstrated significant differences in the distribution of locations between seasons for all packs during period 1 and for four of the six packs during period 2 (Table 2).

Discussion

The existence of long-term spatial stability among coyote home ranges on the PCMS is indicated by the substantial overlapping of period 1 home ranges by period 2 home ranges. In addition, a comparison of the distance between the centroids of pack home ranges showed that the mean distance between the centroids of period 1 and period 2 home ranges was not significantly larger than the distance between the centroids of home ranges of packs between seasons in any one period. Thus, coyote packs on our study site maintained relatively stable territories for over 10 years.

Despite long-term spatial stability of coyote packs in an area, there are a number of factors that may influence short-term changes in space use within that area. The changes in home-range sizes between periods likely reflect short-term changes due to prey availability and distribution, and may have no influence on the level of spatial stability exhibited. Territorial expansion and contraction due to changes in resource abundance or pack dynamics have been well documented in canids and other animals (Fuller and Keith 1980; Messier 1985; Peterson and Page 1988). Fuller (1989) noted that the relatively stable, long-established territorial boundaries of wolves in north-central Minnesota fluctuated little with short-term changes in pack size.

Changes in small-scale space use were also evident in our study, through analysis of the distribution of coyote-pack locations. A number of authors have noted that home ranges of animals are often unevenly used, with animals concentrating their activities in certain areas and using others infrequently (e.g., Macdonald et al. 1980; Voigt and Tinline 1980; Laundre and Keller 1981). This differential use of the home range can vary over time. Significant differences in the distribution of locations for the majority of the coyote packs both between periods and between seasons indicate that coyotes vary their utilization of space within the territory despite maintaining the same site and home-range boundaries over a number of years.

This shift in the distribution of range use may be influenced by changes in prey distribution and abundance, habitat

Fig. 1. Overlapping home ranges of coyote packs in periods 1 and 2 on Pinon Canyon Maneuver Site, Colorado.
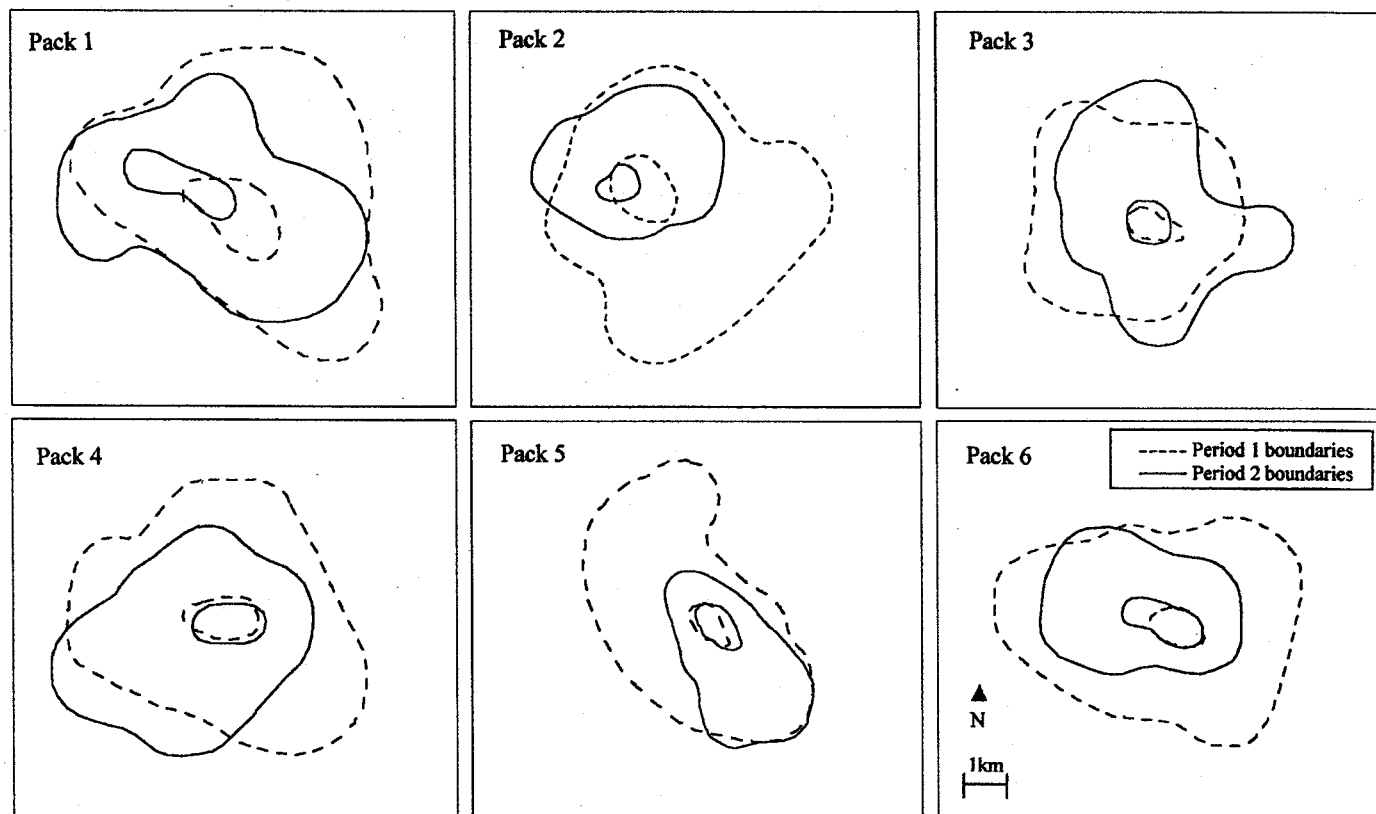

Table 1. Multiple response permutation procedures comparing the distribution of locations of overlapping packs in periods 1 and 2 on the Pinon Canyon Maneuver Site, Colorado.

Pack No.	δ	P
1	16.49	<0.001
2	100.22	<0.001
3	1.06	0.13
4	13.33	<0.001
5	30.60	<0.001
6	20.60	<0.001

Table 2. Multiple response permutation procedures comparing the distribution of locations between seasons within packs in periods 1 and 2 on the Pinon Canyon Maneuver Site, Colorado.

Period	Pack No.	δ	P
1	1	3.71	<0.01
	2	2.64	0.02
	3	4.36	<0.01
	4	2.72	0.02
	5	3.02	0.01
	6	2.07	0.04
2	1	0.56	0.22
	2	12.09	<0.01
	3	32.58	<0.01
	4	19.85	<0.01
	5	0.52	0.23
	6	11.42	<0.01

changes, and intra- and inter-pack dynamics. These variables have been shown to temporally influence space-use patterns in a number of animals. For example, Reid et al. (1994) noted that, in Alberta, space use by river otters (*Lontra canadensis*) was different in winter than in other seasons, owing to the need to find shelter with ready access to water (ice cover makes access to most water bodies problematic in winter). Temporal changes in the spatial distribution and availability of water also influenced the space-use patterns of raccoons (*Procyon lotor*) in Texas (Gehrt and Fritzell 1998). In some species, space use by males has been found to vary with changes in the distribution and density of females (e.g., Nelson 1995). Both lynx (*Lynx canadensis*) and coyotes were shown to shift their habitat-use patterns in response to changing prey (lagomorph) abundance among habitats (Murray et al. 1994). Bekoff and Wells (1986) doc-

umented the differential use of home ranges with seasonal changes for coyotes, whereby the reproductive female spent an almost sixfold increase in time around the denning area during the pup-rearing season compared with other seasons.

Long-term spatial stability is likely an adaptive advantage for coyote packs, owing to increased familiarity with foraging areas and shelter in the territory. A pack exhibiting long-term spatial stability will also gain familiarity with packs holding neighboring territories and with interspecific competitors, which may reduce aggressive intra- and inter-

specific interactions. A knowledge of resource distribution and the presence of potential competitors would be especially beneficial to coyote packs during pup-rearing seasons. Spatial stability in coyote packs may also facilitate stable dominance relationships, which are important for pack cohesiveness and territorial defense (Gese 1998).

The strong spatial stability exhibited by the coyote packs in this study may have been facilitated by the high density of coyotes in the area (Gese et al. 1989; Kitchen et al. 1999). An increase in site-use stability when the density of a population is close to habitat saturation has been documented in a number of animal species (e.g., Sterck 1998). The incidence of movement out of territorial areas by canids seems to increase with the ready availability of suitable resource-rich vacant areas (wolves, Fritts and Mech 1981; dingoes, Thomson et al. 1992). If higher-quality territories are available, remaining faithful to its present site may not be beneficial for an animal (Switzer 1993), although a number of additional variables may influence the adaptive advantage of site stability, including habitat stability (McNicholl 1975) and the variability of the quality of the habitat within the territory (Bench and Hasselquist 1991). Thus, the level of stability in long-term site use among coyote populations may vary with environmental, social, and individual factors.

Knowledge of coyote behavior, such as the spatial stability of home range, is becoming increasingly important in their management, owing to heightened efforts to restrict attempts to control them to localized areas. There is some evidence that coyotes will leave a territory, at least temporarily, to pursue prey (Shivik et al. 1996), or be unable to defend territories containing a large prey base from transients (Camenzind 1978). However, other studies have shown that when breeding coyotes hold territories containing sheep, they are the principal predators of the sheep (Althoff and Gipson 1981; Till and Knowlton 1983; Sacks et al. 1999). Thus, targeting coyotes that hold territories in the immediate vicinity of depredation will be more effective than targeting coyotes over a wider area (Sacks et al. 1999), especially in areas where these coyotes may otherwise hold their territories for a number of years. Alternatively, sterilizing site-faithful breeding coyotes that hold territories containing sheep may reduce depredation (which may occur primarily for pup provisioning) and lessen the chance of reproducing animals becoming established in the area (Till and Knowlton 1983).

The existence of long-term home range stability among coyote packs suggests the possibility of multigenerational site fidelity of packs, with territories being passed on to family members; this has been documented in wolves (Mech and Hertel 1983), jackals (Moehlman 1983), and red foxes (von Schantz 1981). Sharing and, later, inheriting a natal home range can provide an adaptive advantage for offspring in cases where there is little probability of obtaining a territory through dispersal, and may provide opportunities to indirectly increase fitness through assisting in sibling rearing (Myles 1988). Further research is needed to document the level of site inheritance within family groups among coyotes.

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